

# Equus idahoensis from the Pliocene of Arizona, and its role in plesippine evolution in the American southwest

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## ABSTRACT

Later Pliocene and early Pleistocene plesippine equids from western North America have been interpreted to form a morphological lineage native to Idaho: *Equus (Plesippus) shoshonenis* to *E. (P.) stenosis angustus* to *E. (P.) fromanensis*, with the latter species presaging subsequent North American caballine equids such as *E. scotti*. Another large late Pliocene plesippine, *E. (P.) idahoensis*, is also known from western North America, but is not considered a part of this morphocline; the origins and subsequent evolution of this species have not been fully defined.

Renewed field investigations at the Pliocene 111 Ranch locality in Graham County, Arizona have resulted in the recovery of numerous vertebrate fossils, including remains of extinct equids. These newly-recovered fossils augment earlier collections by various institutions over the past several decades. At least three and possibly four or more species of extinct *Equus* (including the subgenus *Plesippus*) are represented in the 111 Ranch assemblage, as is the more diminutive Pliocene equid *Nannippus*.

Large, slender metapodials from 111 Ranch fall within the size range of *Equus idahoensis*. Associated teeth exhibit short protocones in the upper premolars and reduced ectoflexids in the lower molars. These characters also resemble *E. idahoensis*, and so these fossils warrant assignment to that species. Large metapodials from 111 Ranch are also similar in size and proportion to like elements of *E. enormis* from Anza-Borrego, California; however, *E. enormis* exhibits elongate protocones in the upper premolars that are derived relative to *E. idahoensis*. The similarity of these taxa suggests that *E. idahoensis* and *E. enormis* may be closely related, constituting a previously unrecognized Plio-Pleistocene large equid lineage in the southwestern United States – one that parallels the smaller native Idaho plesippines in evolving towards a caballine condition. This interpretation suggests in turn that not all subsequent North American caballine equids can be proposed to derive solely from the Idaho lineage.

## EQUUS IDAHOENSIS

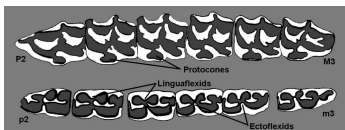


**Figure 1 (above).** UCMP 22348, holotype left P4 of *Equus idahoensis* Merriam, 1918, occlusal and anterior views. From Repenning *et al.*, 1995.

The species *Equus idahoensis* Merriam, 1918 was named from an upper and a lower cheek tooth from the Froman Ferry area, Idaho. Merriam (1918) chose the upper tooth (Figure 1) considered a P4 (Merriam, 1918), a dP4 (Winters, 1985), or a P3 (Repenning *et al.*, 1995)] as the holotype, but this specimen is “wholly inadequate for characterizing the species” (Shotwell, 1970:93).

Schultz (1936) referred large Pliocene equids from Grandview, Idaho to *Equus idahoensis* (Figure 2), but preferred a generic assignment to *Plesippus* Matthew (1924). This referral was based primarily upon the small protocones and the “V”-shaped linguiflexids observed in the Grandview sample as well as other plesippines (Figure 2). Skinner (1972) proposed that plesippines [*Dolichohippus* in Skinner (1972), but see discussions in Forsten and Eisenmann (1995), Repenning *et al.* (1995), Albright (2000), Eisenmann and Baylac (2000), and Scott (2004) on the preferred retention of *Plesippus*] was more appropriately recognized by the depth of penetration of the ectoflexids into the molar isthmus. This feature is present to varying degrees in *E. idahoensis* (Figure 2).

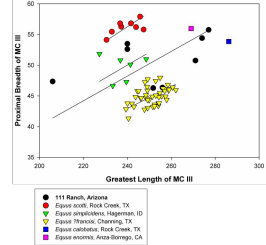
Although the holotype of *Equus idahoensis* is technically inadequate, the species was named prior to the presently accepted strict codification of zoological naming procedures. The association of the nomen with a well-established hypodigm (the large Grandview equids) warrants its continued use, to promote taxonomic stability (ICZN, 2000, Article 75.5), although eventual designation of a suitable neotype is recommended. The amended diagnosis for *E. idahoensis* includes: large size; frequent retention of the P1; moderately developed protocones with small anterior “heels”; generally “V”-shaped linguiflexids; and molar ectoflexids that usually penetrate the isthmus.



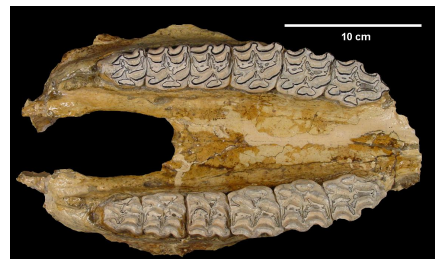
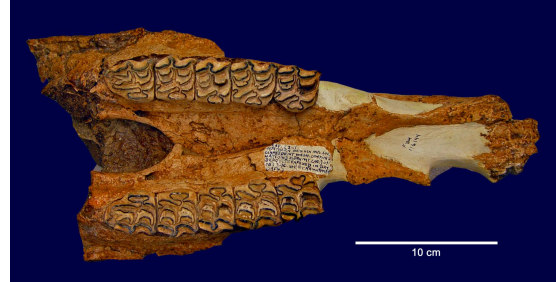
**Figure 2 (left).** Dental morphology of *Equus idahoensis* from Grandview, Idaho (after Schultz, 1936). Black = enamel; dark grey = dentine; white = cementum. Key labels: Protocones, Linguiflexids, Ectoflexids. Note the shortened ectoflexid in m2.

## 111 RANCH, ARIZONA

Vertebrate fossils dating to the later Pliocene ( $\leq 6$  mya) have been previously reported from 111 Ranch in Graham County, Arizona, from excavations over nearly 70 years (Knechtel, 1936; Wood, 1960; Seff, 1962; Lindsay and Tessman, 1974; Galusha *et al.*, 1984). *Equus* spp., *Plesippus* (also as *Dolichohippus* and *Hippogryx*), and the diminutive Pliocene *Nannippus* have been previously reported from 111 Ranch (Lance, 1960; Wood, 1960, 1962; Galusha *et al.*, 1984). At least three and possibly four or more species of extinct *Equus* [including *Equus (Plesippus)*] are represented, in addition to *Nannippus*.



**Figure 4.** *Equus* from 111 Ranch, Arizona. Left: metacarpal series, dorsal view. Above: bivariate plot of metric data from 111 Ranch metacarpals, plotted against other Plio-Pleistocene *Equus*.



## EQUUS ENORMIS FROM ANZA-BORREGO DESERT STATE PARK

Large equid fossils from the Plio-Pleistocene Huaco Formation in the Anza-Borrego Desert State Park (ABDSP), San Diego County, California were established as the species *Equus enormis* Downs and Miller, 1994. These fossils are similar to *E. idahoensis*, but are slightly larger and more derived. Although considered a plesippine, the protocones of *E. enormis* have marked anterior development, particularly in the premolars, closely resembling that of later North American Pleistocene equids such as *E. scotti* (Scott, in press) (Figure 6). Further, the molar ectoflexids of *E. enormis* do not fully penetrate the molar isthmus as in other plesippines such as *E. simplicidens*; rather, the degree of ectoflexid penetration resembles some specimens of *Equus scotti* (Scott, in press) (Figure 6). Limb elements assigned to *E. enormis* are similar in size to like elements of *E. idahoensis* (following Shotwell, 1970) (Figure 7).

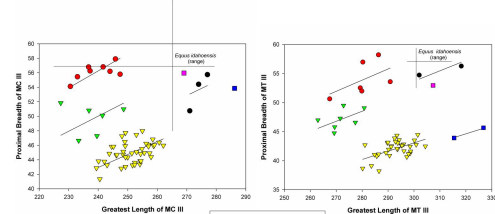
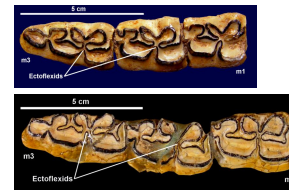
**Figure 3 (right).** Theodore Galusha of the American Museum of Natural History (AMNH) collecting fossils at 111 Ranch circa 1977. Collections from 111 Ranch are housed at the AMNH, the University of Arizona Laboratory of Paleontology (UALP), the Sam Noble Oklahoma Museum of Natural History (OMNH), and the Mesa Southwest Museum (Mesa SW). Inset: location of 111 Ranch.



## EQUUS IDAHOENSIS FROM 111 RANCH

Because the majority of the equid fossils identified from 111 Ranch consist primarily of isolated elements, particularly cheek teeth, reliable species assignments are difficult to advance. However, specimen FAM 116144 – consisting of a partial skull, a partial right dentary, and a right MC III (Figure 5) of what is presumed to be a single individual – is listed in the collections of the American Museum of Natural History (AMNH) as *Equus idahoensis*, although this identification (presumably advanced by M. Skinner) has not previously been published and the rationale behind the identification is not known. The present study examined FAM 116144 in the collections of the AMNH, and confirmed that referral to *E. idahoensis* was justified. Of particular note was the size of the right MCIII, which fell within the “core” published range for *E. idahoensis* (Shotwell, 1970) (Figure 7). Additionally, the morphology of the upper cheek teeth and the lower molars very closely resembled published descriptions and figures for *E. idahoensis* (compare Figure 5 with Figure 2), although the molar ectoflexids were somewhat reduced in length, likely due to ontogenetic wear. The fortuitous confluence of elements and features from this individual permits a confident assignment to species, whereas consideration of any one or two of these elements in isolation would likely have precluded such an assignment.

**Figure 5.** *Equus idahoensis* from 111 Ranch, Arizona. Left: FAM 116144, partial skull with L&R P3-M3, occlusal view, showing primitive premolar pattern consistent with *E. idahoensis* (compare with Figures 1 and 2). Anterior is to the right. Below: FAM 116144, lower right molars, occlusal view, showing derived ectoflexids (compare with Figure 2). Right: FAM 116144, R MCIII (L of *E. idahoensis*, compared to ABDSPV (IVCM) 15/32-12, paratype L MCIII (R of *E. enormis*, dorsal view).



**Figure 7.** Bivariate plots of measurements for MCIII (above) and MTIII (below) right for *Equus idahoensis* from 111 Ranch, plotted against other Plio-Pleistocene *Equus*. Note the similarity to *E. enormis*.

**Note:** The seemingly anomalous size range for MCIII of *Equus idahoensis* (above left; after Shotwell, 1970) may include more than one species, or may result from a typographical error. The sample was not re-examined for the present study.

## SIGNIFICANCE OF EQUUS IDAHOENSIS FROM 111 RANCH

The identification of *Equus idahoensis* from 111 Ranch is important for several reasons. First, the species has not previously been confirmed from this locality, and is very poorly known from elsewhere in the American southwest, with only a few reports based upon remains of limited diagnosticity (Azzaroli and Voorhies, 1993; Albright, 2000). Secondly, previous specific assignments of fossils of *Equus* from 111 Ranch (e.g., Galusha *et al.*, 1984) have been presented in faunal lists, with no systematic descriptions; these records must be considered provisional and await confirmation. The present study therefore presents the first definitive species assignment for any *Equus* from 111 Ranch. Third, the fossils under study here are significant due to their proximity geographically, temporally, and morphologically to fossils of *E. enormis* from the ABDSP. Both species have previously been considered plesippine (e.g., Schultz, 1936; Downs and Miller, 1994; Repenning *et al.*, 1995), but both share several characteristics that distinguish them from earlier plesippines (e.g., *E. simplicidens* and *E. shoshonenis*). These features include large size, more derived protocones (even in later wear), and ectoflexids that do not fully penetrate the molar isthmus. In each of these features, *E. enormis* appears further derived relative to *E. idahoensis*. These features also resemble equids such as *E. scotti*.

## PLESIPPINES AND CABALLINE EQUID EVOLUTION

Later Pliocene and early Pleistocene plesippine equids from northwestern North America have been interpreted to form a morphological lineage native to Idaho (Repenning *et al.*, 1995): *Equus (Plesippus) shoshonenis* to *E. (P.) stenosis angustus* to *E. (P.) fromanensis*. This evolutionary trend was proposed as presaging later North American caballine equids such as *E. scotti*. *E. idahoensis* (as *Plesippus idahoensis*) was not considered part of this morphocline, but was separated due to its larger size, straighter teeth, and relatively small but non-tapering protocones (Repenning *et al.*, 1995). *E. idahoensis* was interpreted to have entered the western Snake River Plain after ~2.3 mya, at which time the *E. (P.) shoshonenis* > *E. (P.) stenosis angustus* > *E. (P.) fromanensis* lineage bifurcated, dispersing into Eurasia to eventually evolve into the extant zebra species *E. (Dolichohippus) grevyi*, and in North America, evolving towards later Pleistocene caballine equids such as *E. scotti* (Repenning *et al.*, 1995).

The observed metric and morphologic similarities between *Equus idahoensis* and *E. enormis*, as well as their temporal and (as demonstrated herein) geographic proximity, suggest that the two species may be closely related. Further, dental characters in these species appear to stand midway between the more primitive plesippine condition and the more derived caballine form. In this manner, *E. idahoensis* and *E. enormis* parallel the plesippine-caballine morphocline proposed for the native Idaho equids (Repenning *et al.*, 1995). Azzaroli and Voorhies (1993) recognized the apparent transitional nature of *E. idahoensis* between plesippines and later caballines, but did not compare the species with fossils from the ABDSP (*E. enormis* having not yet been named). Albright (2000:99) suggested that *E. idahoensis* (as “*Plesippus idahoensis*”) “may have been a member of the same lineage that gave rise to *E. enormis*”, but this view was advanced based upon early Pleistocene teeth from southern California, at least one of which (UCMP 322602, R P4) is distinctly non-plesippine in morphology and is probably better referred to *E. scotti*. The present study confirms the presence of *E. idahoensis* in the American southwest, proposes a close relationship between this species and *E. enormis*, and suggests that the cabaline tendencies of these related species negate the interpretation that all later North American caballines can be assumed to derive solely from the native Idaho lineage espoused by Repenning *et al.* (1995).

## REFERENCES

Albright, L.B. 2000. Biogeographic and vertebrate paleontology of the San Timoteo Shoshonean, southern California. *University of California Publications, Geological Sciences*, Volume 104, 321 p. 7-9.

Azzaroli, A. and M.R. Voorhies, 1993. The genus *Equus* in North America: the Blumstein Shoshonean. *Paleontological Journal* 80: 175-198.

Downs, J. and C.J. Miller, 1994. Late Cenozoic equids from the Anza-Borrego Desert of California. *Natural History Museum of Los Angeles County Contributions in Science* 440: 1-40.

Forsten, A. and W. Bayle, 2000. Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: a morphometric analysis of the eulagone. *Equine Veterinary Science* 28(2): 89-98.

Forsten, A. and V. Eisenmann, 1995. *Equus (Plesippus) simplicidens* Cope, and *Dolichohippus* (Mammalia 90(1): 85-88.

Galusha, T., N.M. Adams, E.H. Lindsay, R.L. Galusha, and R.H. Tiedel, 1984. Biogeographic and morphogenetic history, late Pliocene rocks, 111 Ranch, Arizona. *Geological Society of America Bulletin* 95: 178-222.

Knechtel, M.H., 1936. Geology and ground-water resources of the valley of Gila River and San Simon Creek, Arizona. United States Geological Survey Water Supply Paper 764-T, 103-222.

Lance, J.F., 1960. Stratigraphic and structural position of Cenozoic basal beds in Arizona. *American Geological Society* 1: 158-159.

Lindsay, E.H. and N.T. Tessman, 1974. Cenozoic vertebrate localities and faunas in Arizona. *Journal of the Arizona Academy of Science* 10(1): 3-24.

Matthew, W.D., 1924. A new link in the ancestry of the horse. *American Museum Novitates* 131: 1-2.

Nelson, J.C., 1974. New Materials from the Idaho Pliocene. *University of California Publications, Bulletin of the Department of Geology* 12(2): 123-150.

Repenning, C.A., F.R. Winters and G.R. Scott, 1995. The early Pleistocene faunal element – radiolarian biogeography of Froman Ferry, Idaho and the Gila River Formation, southwestern Idaho. *United States Geological Survey Bulletin* 2580: 80 p.

Scott, E., 2004. Pliocene and Pleistocene horses from Panguitch, Utah. In: A.D. Barnard and J. Bredemeyer (eds.), *Biodiversity Response to Environmental Change in the Middle Pleistocene: The Panguitch Case Study from Colorado*. Boulder: University of Colorado Press, 24-27.

Scott, E., in press. Extinct horses and their relatives. *Fossil Treasures of the Anza-Borrego Desert: The Last Seven Million Years* (G.T. Jefferson and L. Lindsay, eds.).

Seff, P., 1962. Stratigraphic geology and depositional environments of the 111 Ranch area, Graham County, Arizona. Unpublished PhD dissertation, University of Arizona.

Shotwell, J.A., 1970. *Plesippus* mammals of southern Oregon and adjacent Idaho. *Bulletin No. 17*. Museum of Natural History, University of Oregon, 100 p.

Skinner, M.F., 1972. *Equus* (Perissodactyla). In: M.F. Skinner and C.W. Hibbard (eds.), *Early Pleistocene prehistoric and geologic notes and faunas of north-central Nebraska. Bulletin of the American Museum of Natural History* 140: 3-148.

Winters, M.R., 1985. *Review of North American fossil species of the genus Equus (Mammalia, Perissodactyla) Equidae*. Unpublished PhD dissertation, University of Arizona, 24 p.

Wood, P.A., 1960. Paleontological investigations in the 111 Ranch area. *Arizona Geological Survey Bulletin* 1: 141-143.

Wood, P.A., 1962. Pliocene faunas from the 111 Ranch area, Graham County, Arizona. Unpublished PhD dissertation, University of Arizona, 127 p.

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